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XVII.—*Further Notes on the Anatomy and Development of Scorpions, and their bearing on the Classification of the Order.*

By Malcolm Laurie, B.A., D.Sc., F.R.S.E., F.L.S., Professor of Zoology at St. Mungo's College, Glasgow.

[Plate IX.]

Since the publication of my former notes on this subject * I have had an opportunity of examining a number of species of Scorpions belonging to typical genera. This opportunity I owe to the kindness of Mr. Pocock, of the British Museum, and I gladly take this opportunity of thanking him. While sufficient material has not yet been examined to enable me to base a complete classification on it, nevertheless a number of interesting facts have been ascertained with regard to the development, and it seems better to publish these without waiting for the problematical arrival of further material. This is the more advisable as I find it necessary now to revise some of the conclusions to which my earlier observations seemed to lead. As a general result I am more than ever convinced of the great value of the mode of development as a basis for classification, and am inclined to consider the structure of the lung-book lamellæ of subordinate but considerable value.

* Ann. & Mag. Nat. Hist., March 1896.

I. The Lung-books.

The results of an examination of the lung-books of a few forms in addition to those described in my previous paper may be very briefly stated. They all came under two types :—

(1) *Spinous type.*

Scorpionidæ: *Ischnurus ochropus*, Koch; *Hadogenes troglodytes* (Pet.); *Hemiscorpius lepturus*, Pet.
Iuridæ: *Anuroctonus phœodactylus* (Wood); *Broteas Herbsti*, Thor.
Bothriuridæ: *Cercophonius squama* (Gerv.).

(2) *Reticulate type.*

Butheolus thalassinus, Sim.; *Heterocharmus cinctipes*, Poc.; *Chœrilus variegatus*, Sim.

The reticulate forms are of special interest. Hitherto I have only found this structure in the Buthidæ, and am inclined to consider it as characteristic of them. *Butheolus* and *Heterocharmus* are both somewhat aberrant forms of this family. *Heterocharmus* has a pentagonal sternum, and its close ally (if, indeed, the two are distinct genera), *Charmus*, Karsch, was placed by its author in the subfamily Iurini of the Pandinoidæ of Thorell. The possession of reticulate lung-book lamellæ is strong confirmation of the accuracy of their present position. *Chœrilus variegatus* is also an aberrant form, having among other points of interest circular stigmata. Pocock places it in a subfamily by itself among the Iuridæ, but its position seems somewhat uncertain, and the lung-books are strong evidence in favour of a relationship to the Buthidæ.

II. Development.

The terms I have hitherto used to define the two chief types of development will no longer serve, because there are so many variations from the type in each case that to speak of *Scorpio* and *Euscorpius* types of development is misleading. The fundamental difference is that while in the one case, what I have described as the *Euscorpius* type, the egg early leaves the follicle in which it is formed and passes into the cavity of the ovarian tube, in the other case (*Scorpio* type) the egg develops *in situ*, and as the embryo becomes too large for

the follicle it extends down and occupies a diverticulum from the ovarian tube, at the distal end of which the egg is originally formed. I would suggest apoikogenic and katoikogenic * as, for the present, adequately designating the two modes. The katoikogenic (*Scorpio* type) forms are always, so far as observation has yet gone, devoid of any appreciable amount of food-yolk. The apoikogenic ones, on the other hand, usually contain a large amount of food-yolk, but, as we shall see, there are certain exceptions (*Scorpiops*, *Vejovis*, &c.). In the apoikogenic forms also there appears always to be a double embryonic membrane formed at an early stage, the outer layer of which, usually termed the serous membrane, is easily distinguished by its large cells containing enormous flattened nuclei. I have been unable to find these membranes in the katoikogenic embryos.

The diverticula at the ends of which the katoikogenic eggs are formed seem always to terminate in a solid cord of cells—the appendix. The central core of this appendix consists of cells characterized by thick, highly refractive cell-walls and little or no protoplasm. These cells appear to form a means of communication down which the nutritive secretion passes from the outer cells of the appendix to the embryo. The material supplied in this way is usually taken in through the mouth of the embryo, which is one of the earliest structures to be developed. Some of the further specializations for the nutrition of the embryo in these katoikogenic forms are described below. They form a most interesting series, and, taken along with the forms I have previously described †, seem to afford a good basis for classification.

A. Apoikogenic Forms.

Scorpiops Hardwickii (Gerv.).

The embryos of this species appear at first sight quite similar to those of *Euscorpius*, their position in the ovarian tube being marked in my specimen by oval swellings about 2 millim. long and 1 millim. wide. Sections, however, show that while this form agrees with *Euscorpius* in the place in which the embryo develops, it differs markedly from it in the type of development. We find the inside of the swelling on the ovarian tube lined throughout by a double cellular

* From ἄποικος, away from home, and κάτοικος, at home.

† "Development of *Scorpio fulvipes*," Quart. Journ. Micr. Sci. vol. xxxii.; "Some newly-hatched Specimens of *Opisthophthalmus*," Proc. Roy. Phys. Soc. Edinb. 1896.

membrane, the outer layer of which is easily recognized by the enormous flattened nuclei of the cells as the "serous membrane," the inner membrane being the amnion. In *Euscorpius* we find these two membranes closely surrounding the embryo, and in early stages extending beyond the embryonic area over the yolk. In *Scorpiops*, however, there is no yolk, and the membranes surround a space at one end of which the embryo is developing. My specimen was in a comparatively young stage, and the embryo only occupied about one fourth of the space surrounded by the embryonic membranes. The walls of the ovarian tube are very thick and the cells probably secrete nourishment.

As there were embryos present there were only eggs in a very early stage of formation. Judging from them, the eggs seem to be formed in a pedunculated follicle, and not sessile on the ovarian tube, as in *Euscorpius*.

This type of development brings this form into close relationship with *Vejovis*, in which, as I pointed out in my former paper, there is little or no yolk. The absence of yolk and the pedunculated ovarian follicles give us a transition form towards the katoikogenic type of development.

Iurus Dufoureius (Brullé). (Pl. IX. fig. 1.)

Of this form I have unfortunately not been able to get any embryos. The ovarian tube (fig. 1) is very large and contains a considerable amount of coagulum. The unfertilized ova of my specimen are very small, measuring ·15 millim. by ·1 millim. They are contained in a follicle borne on a stalk, and in this, as in their small size, resemble the structure found in *Scorpiops*. I believe the ova were ripe and had attained their full size, because the surrounding follicle-cells were apparently degenerating. I have no doubt the development will prove to be very similar to that of *Scorpiops*.

B. Katoikogenic Forms.

Hemiscorpius lepturus, Pet. (Pl. IX. fig. 2), and *Diplocentrus Whitei* (Gerv.).

Of these two genera, representing subfamilies in Pocock's classification, I have only been able to get ovaries containing unfertilized eggs.

The structure of the diverticulum, appendix, &c. in both these species so closely resembles that of *Scorpio* and other forms that I have no doubt the development is katoikogenic, but no further details could be ascertained.

Urodacus novæ-hollandiæ, Pet. (Pl. IX. figs. 3 *a–d*.)

The embryos of this form in my possession are in an advanced stage of development, the eyes, limbs, &c. being all well formed; they measure about 12 millim. in length and are markedly cylindrical. The appendix is short and there is a well-marked thickened portion at the top of the diverticulum. Removed from the follicle the embryo appears as in figs. 3 *b* & *c*. The cheliceræ project straight out in front and are of considerable length, terminating in a cup placed towards the inner side. From this cup an incomplete groove seems to run between the two cheliceræ down towards the mouth. This groove is partly closed in at its posterior end by processes from the basal joints of the chelæ (fig. 3 *c*). The central cord of the appendix terminates close to the distal end of the cheliceræ.

The chelæ have their elbows well forward in front of the carapace and project into a fold of the surrounding diverticulum, as is indicated by the dotted line in fig. 3 *b*. The inside of this fold is lined with apparently actively secreting cells. Fig. 3 *d* is a section across just above the elbows of the chelæ and shows the structure of this part of the diverticulum and also that of the lower part of the appendix and the cheliceræ. The secretion from these cells at the upper end of the diverticulum is probably for the most part absorbed by the mouth, there being nothing in the structure of the chelæ to indicate absorption as one of their functions. Secretion by the top of the diverticulum is, I think, a somewhat primitive mode among these katoikogenic forms, as it is only continuing to a somewhat later stage the mode by which the embryo is nourished in its early stages before the mouth is formed. The arrangement of the cheliceræ leads towards the state of affairs we find in *Ischnurus*, while the method adopted by *Hormurus* derives itself from the secreting upper part of the diverticulum.

Ischnurus ochropus, Koch. (Pl. IX. figs. 4 *a–e*.)

The embryos of *Ischnurus* are in an advanced stage and measure 10 millim. in length, while the appendix at the distal end of the follicle measures about 3 millim. The form of the appendix differs from that of *Scorpio* in that it is not spirally twisted on itself and has a distinct dilatation on it. On removing the follicle, which can be done without much difficulty, the first point that strikes one is the hairiness of the embryo. The segments behind the carapace, which are

cylindrical in shape, are liberally sprinkled with dark yellow curved bristles; these bristles are not simple, but have three or four small protuberances near the base (fig. 4 *e*). When we come to examine the front end of the embryo we find that the chelicerae are inserted wide apart under the angles of the carapace, and lie sloping towards one another in an almost transverse position (fig. 4 *b*). From the end of each there runs a thin process, and these two processes lying close together in the middle line pass forward into the appendix, lying dorsal to the central cord. On tracing one of these processes forward in a series of sections, for I have not been able to dissect out the whole of their course, we find it runs as a simple process till it comes to the dilated part of the appendix. On reaching that, however (fig. 4 *d*), it expands and bifurcates, forming a pair of somewhat irregular plates, which come into close relation with an oval mass of cells. It is beyond question, I think, that these processes must serve to absorb nutritive material from the surrounding cells. It was impossible to make out any details of the histology of these organs beyond the fact that each plate is formed of a thin outer cuticle, lined by a layer of flattened cells with large spherical nuclei. In the middle there seems to be a space filled with granular material, which may be coagulum.

The central cord is thick in the upper part of the appendix, but becomes very small as it runs down towards the embryo. It ends some little way in front of the body of the embryo and is not grasped and masticated by the chelicerae, as in *Scorpio*. There is no special development of secreting cells round the upper end of the diverticulum, such as we find in *Urodacus*.

Opisthocentrus madagascariensis (Kraep.).

This form is practically the same as *Ischnurus*. The chelicerae are continued forwards on each side of the central cord into the appendix; they do not, however, run so far up as in *Ischnurus*, and the continuations are simple instead of being divided up. These two differences, however, are very possibly due to the embryo being considerably younger. The front of the cephalothorax projects forward a considerable distance beyond the mouth, and may be partly absorptive in function. The central cord is coiled in the thick part of the appendix and runs back ventral to the chelicerae as far as the mouth.

Hormurus australasiæ (Fabr.). (Pl. IX. figs. 5 *a*, *b*.)

This form was represented among my specimens by some moderately advanced embryos. The appendages are quite distinct, but the eyes have not yet appeared. The diverticula measure about 4 millim. in length and are peculiar in having only a rudimentary appendix. The mode of nutrition is quite peculiar. The cheliceræ are short and in no respect unusual in form, while the chelæ are unusually large. The last joint of the chelæ runs forward close to the middle line and becomes associated with a mass of large granular cells, which look more like young ova than anything else (fig. 5 *b*, *sc.*). The association is very close, as the chela is drawn out into processes which run in among the cells. These cells occupy a pocket on the ventral side of the top of the diverticulum; they differ from the secreting cells which occupy a somewhat similar position in *Urodacus* in structure and in being confined to the ventral side, instead of extending as a collar all round. There is a dorsal pocket (fig. 5 *b*, *sc'*), also apparently lined by secreting cells, which are more like those of *Urodacus*, but there seem to be no special absorptive organs connected with it.

Palamnœus Thorellii, Poc. (Pl. IX. fig. 6.)

This form agrees more closely with *Scorpio* and *Opisthophthalmus* than with any of the others which I have examined. The free segments grow out into dorsal processes, which in the not very advanced stage in my possession are small, but probably increase in size from this stage on. The cheliceræ are in the form of a pair of enormous conical structures, the internal face of each being flattened and longitudinally grooved. The grooves are lined with chitin, and in the tube formed by the apposition of the grooves lies the central cord of the appendix, which is masticated by the cheliceræ. The enormous size of these appendages is the most striking feature of these embryos, and suggests that a mode of nourishment like that in *Urodacus* was the earlier arrangement, and that this chewing of the central cord is derived from it, *Palamnœus* being in this case an intermediate form between *Urodacus* and *Scorpio*, in which last the cheliceræ are much smaller and more purely masticatory.

If, now, we try to apply the above observations to the classification of the order the result is as follows. I take as a

basis Pocock's classification *. I have enclosed in parentheses the names of those genera which I have not had an opportunity of examining, and their position is in some cases doubtful. So far as observation has gone the members of the family Scorpionidæ are all characterized by the katoikogenic mode of development, the other families—Iuridæ, Bothriuridæ, and Buthidæ—being apoikogenic.

Fam. I. **Scorpionidæ.**

Subfam. 1. *Scorpionini.*

Scorpio, (*Heterometrus*), (*Miœphonus*), (*Œcopetrus*), *Opisthophthalmus*, *Palamnœus.*

In this subfamily the cheliceræ masticate the central cord and there are dorso-lateral outgrowths from the free segments. The lung-book lamellæ have spiny free margins. *Opisthophthalmus* might be erected into a separate subfamily on the strength of the extraordinary outgrowths from the carapace and prostomium. *Scorpio*, however, shows an approach to the prostomial outgrowth.

Subfam. 2. *Ischnurini.*

Ischnurus, (*Opisthacanthus*), *Opisthocentrus*, (*Cheloctonus*), (*Chiromachus*).

In this subfamily the cheliceræ send root-like processes forward into the appendix, as described above. The lung-books are spinous. This is Pocock's subfamily minus *Hormurus* and *Iomachus*, along with which some of the other genera ought possibly to go.

Subfam. 3. *Hormurini*, nov.

Hormurus, (*Iomachus*).

The characteristic feature here is the absorption of nourishment by the chelæ, as described above. The lung-books are spinous. *Iomachus* seems, from Pocock's description, more closely allied to *Hormurus* than to the Ischnurine series.

Subfam. 4. *Diplocentrini*, Pocock.

Diplocentrus, (*Oiclus*), *Nebo*, (*Cyphocentrus*).

Nothing is known in this subfamily of the later embryonic

* Ann. & Mag. Nat. Hist. ser. 6, vol. xii. Kraepelin's arrangement (Hamb. Wiss. Anst. 1890 and 1893), which is later, is almost identical as regards the main groups.

stages, and the ovary has been seen only in *Diplocentrus*. The edges of the lung-book lamellæ have an arcade structure in *Diplocentrus* and *Nebo*.

Subfam. 5. *Hemiscorpiini*, Pocock.

Hemiscorpius.

Here also only the ovary is known. The lung-book lamelkæ are spinous. I leave the subfamily because there is no evidence to justify me in altering it, though Kraepelin places the one genus among the Ischnurini.

Subfam. 6. *Urodacini*, Pocock.

Urodacus, (*Iodacus*), (*Ioctonus*).

The cheliceræ form a channel for the secretions of the appendix, and there are also secreting cells round the top of the diverticulum. The lung-book lamellæ are spinous.

The above observations all agree with Pocock's family Scorpionidæ, and consequently tend to support his view as to the importance of the pedal spur as a systematic character.

The alterations above are comparatively slight, only one new subfamily being constituted. Further knowledge would, however, probably lead to other minor alterations.

The remaining forms seem all to be apoikogenic. Pocock's Iuridæ seem to require a great deal of alteration, the other two families remaining almost as they are in his classification. The following is what I would suggest as a provisional arrangement :—

Fam. II. **Iuridæ** = Subfam. *Iurini*, Pocock,
Vejovini, Kraepelin.

The character I depend on here is the apoikogenic development combined with the small size and comparative or absolute absence of yolk in the egg.

Subfam. 1. *Iurini* = *Iurini*, Thor., + *Caraboctonus*.

Iurus, (*Uroctonus*), *Caraboctonus*.

This subfamily is characterized by the arcade structure of the free edges of the lung-book lamellæ. I have not seen the ovary of *Caraboctonus*.

Subfam. 2. *Vejovini*=Vejovoidæ, Thor., + *Scorpiops*, *Anuroctonus*, and *Hadruroides*.

Vejovis, *Scorpiops*, *Anuroctonus*, *Hadrurus*, (*Hadruroides*).

The lung-book lamellæ in this subfamily are spinous along the margin. The ovaries of *Anuroctonus* and *Hadrurus* have not been seen.

Fam. III. **Chactidæ**=*Chactini*, Poc.

Apoikogenic forms with large yolky egg.

Subfam. 1. *Euscorpiini*.

Euscorpius.

Arcade structure of lung-book lamellæ.

Subfam. 2. *Chactini*=*Chactini*, Pocock,—*Euscorpius*.

(*Chactas*), (*Hadrurochactas*), (*Heterochactas*), (*Teuthraustes*), *Broteochactas*, *Broteas*.

Spinous margin to lung-book lamellæ.

It is quite possible, though I do not think very probable, that further light on the development may tend to associate the Euscorpiini and Iurini as against the Chactini and Vejovini. This would seem to be making the structure of the lung-books of greater importance in this case than the mode of development.

Fam. IV. **Bothriuridæ**, Sim.

Bothriurus, (*Brachistosternus*), (*Mecocentrus*), *Cercophonius*, (*Timogenes*), (*Thestylus*), (*Urophonius*), (*Phoniocercus*), (*Centromachus*).

I have only seen the ovary of *Bothriurus* and the lung-books of that species and *Cercophonius*. The eggs are large and spherical and the lung-books spinous.

I have some doubts as to whether this family and the Chactini ought not to be united. The shape of the sternum seems not to be so reliable a test of affinity as used to be supposed.

Fam. V. **Buthidæ** = Buthidæ, Sim., + *Chærilus*.

This family is characterized by a yolky egg, apoikogenic development, and the reticulate type of lung-book lamellæ.

Subfam. 1. *Chærilini.*

Chærilus.

Of this very peculiar genus I have only seen the lung-books, and it is with some misgivings that I place it here on account of their structure.

Subfam. 2. *Buthini* = Buthidæ, Sim.

(*Prionurus*), *Buthus*, *Parabuthus*, (*Grosphus*), *Butheolus*, (*Archisometrus*), (*Isometroides*), *Uroplectes*, (*Tityobuthus*), (*Pseudobuthus*), *Isometrus*, *Tityus*, *Centrurus*, (*Heteroctenus*), (*Ananteris*), (*Charmus*), *Heterocharmus*, (*Stenochirus*).

Looked at from the point of view of the evolution of the order there is little doubt but that the apoikogenic type of development is the most primitive. It is only one step from the laying of the eggs, which is the almost universal custom among Arthropoda. *Peripatus*, *Galeodes*, some Diptera, and some of the mites form exceptions to this habit, but in some of them the internal development is evidently secondary. Further, the eggs containing a considerable amount of yolk are probably nearer the primitive type than those in which the yolk is absent. This, indeed, is necessarily so if the laying of the eggs was the primitive habit. This makes the Chactidæ, Bothriuridæ, and Buthidæ the more primitive forms in these respects.

With regard to the structure of the lung-books, I am inclined to consider the "spinous" type as the original. The reticulate type is more complicated, having pillars over part of its surface and a network of ridges over the rest. The "arcade" margin must have arisen from the "spinous" in two or three separate sections, as it seems impossible to connect *Euscorpius*, *Iurus*, and *Diplocentrus* genetically to the exclusion of the other forms. In this case we are left with probably the Chactini as our starting-point, the highly modified sternum seeming to exclude the Bothriuridæ. From this would diverge four lines of descent—Buthidæ, Bothriuridæ, *Euscorpius*, and Iuridæ. The Iuridæ, of which the Vejovini are the more primitive, lead to the katoikogenic

Scorpionidæ. More evidence is wanted before we can judge of the true relation of the various subfamilies of the Scorpionidæ to each other; but of those I have examined I am inclined to place the Urodacini as the lowest. The secretion of nutritious material by a large section of the diverticulum is what one would expect as the earlier form *. Distinctly divergent lines from this point are shown by the Diplocentrini, Hormurini, Ischnurini, and Scorpionini. Further material is still wanted before many of the forms can be placed, and I have perhaps tried to base too much on a comparatively small number of observations. Doubtless the criticism of other workers in the group will soon correct any points in which I have erred.

EXPLANATION OF PLATE IX.

Lettering throughout.

i. Cheliceræ.
ii. Chelæ.
iii.–vi. The walking-legs.
c. c. Central cord of appendix.

Fig. 1. *Iurus.* Transverse section of ovarian tube and egg, × $\frac{50}{1}$.

Fig. 2. *Hemiscorpius.* A diverticulum with unfertilized egg, × $\frac{10}{1}$.

Fig. 3. *Urodacus.*

3 *a*. Portion of ovarian tube with diverticulum containing embryo, × $\frac{2}{1}$.

3 *b*. Dorsal view of carapace and anterior appendages, × $\frac{10}{1}$. The dotted line shows the way the walls of the appendix are folded.

3 *c*. Ventral view of the same.

3 *d*. Transverse section through top of diverticulum and lower part of appendix, × $\frac{45}{1}$.

Fig. 4. *Ischnurus.*

4 *a*. Portion of ovarian tube and diverticulum containing embryo, × $\frac{2}{1}$.

4 *b*. Dorsal view of embryo. The forward continuations of the cheliceræ are broken short. × $\frac{10}{1}$.

4 *c*. One of the cheliceræ, × $\frac{30}{1}$.

4 *d*. Section through appendix showing continuation forward of the cheliceræ (i.). The appendix, being curved, is cut in two

* Is it possible that the loss of yolk was an adaptation to a climate with short summer and long winter, the provision of nourishment for the embryo being thrown on the period when food was abundant instead of yolky eggs being formed during hibernation?

places, one transverse and the other somewhat oblique. $\times \frac{50}{1}$.

4 *e*. One of the bristles of the embryo, highly magnified.

Fig. 5. *Hormurus australasiæ.*

5 *a*. Ventral view of anterior part of embryo. The cheliceræ are concealed by the large chelæ. $\times \frac{30}{1}$.

5 *b*. Transverse section through distal part of chelæ and the secreting cells (*sc*) surrounding them. *sc'*, dorsal secreting cells. $\times \frac{125}{1}$.

Fig. 6. *Palamnæus Thorellii.* Dorsal view of embryo $\times \frac{10}{1}$.

XVIII.—*On the Synascidia of the Genus* Colella *and the Polymorphism of their Buds.* By M. Maurice Caullery *.

The genus *Colella*, created by Herdmann for the Synascidia collected by the 'Challenger' expedition, belongs to the family of the Distomidæ, and is very nearly related to *Distaplia.*

Among the compound Ascidians in the Museum, the study of which has been entrusted to me by M. Edm. Perrier, there are a certain number of representatives of this genus, some of them from Australia ('Astrolabe' expedition), others from Cape Horn. Thanks to this material, I have been able to obtain a certain number of facts connected with the anatomy, relationships, and blastogenesis of these animals, which I shall set out later in detail. Here I shall only point out the following:—

(1) The species which I have had under examination present all four rows of pores. A specially characteristic arrangement is to be noticed: the second and the third row separate one from the other in the portion near to the endostyle in such a manner as to leave between them a triangular space, not perforated by pores. The pores are not divided into two halves by a transverse band, as in the *Distaplia.* These two characters appear to me to be very suitable as a definition of the genus *Colella.*

(2) The examples of Corms which I have examined are unisexual, a fact already determined by Herdmann for several species; further, in a female Corm the buds only present ovules, in a male Corm only spermatic vesicles; so that, so far as the material at my disposal would allow me to do so, I conclude that there is for each Corm a defined sexuality,

* From the 'Comptes Rendus,' tome cxxii. 1896, pp. 1066-1069.